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AGONISTIC INTERACTIONS BETWEEN FEMALE BOWL AND DOILY SPIDERS (ARANEAE, LINYPHIIDAE): OWNER BIASED OUTCOMES

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ABSTRACT

Stereotypic agonistic behavior was observed in induced encounters involving female bowl-and-doily spiders (*Frontinella pyramitela*: Linyphiidae) at natural web sites. Relative size (mass) of opponents, resident status, and web size were examined as possible assessment parameters influencing interaction outcome. Web owners won significantly more interactions than did intruders, regardless of the relative sizes of the spiders. The area of the sheet-web had no relationship to interaction outcome.

INTRODUCTION

Agonistic interactions between spiders occur in two basic contexts: disputes between males over access to a female (Rovner 1968; Dijkstra 1969; Aspey 1976, 1977; Austad 1983; Suter and Keiley 1984) and territorial conflicts over web sites (Buskirk 1975; Ross 1977; Riechert 1978, 1979, 1982; Wise 1983). Among recent approaches to the study of animal conflict behavior is the use of game theory to predict which animal will win or lose (Maynard Smith 1974; Riechert and Hammerstein 1983; Parker 1984). Maynard Smith and Price (1973) have proposed the "hawk-dove" game as a standard paradigm for animal conflict, with the simplest case involving adoption of either an aggressive or a nonaggressive strategy. Use of the appropriate strategy should minimize contest cost and risk of injury to both contestants. The strategy adopted is generally associated with differences in fighting ability and/or in rewards associated with winning. These differences determine the "relative holding power" (RHP = probability of winning) of an individual. Game theory predicts that individuals involved in territorial disputes will assess their own RHP and use the behavioral strategy appropriate to this status (Parker 1974). These concepts have been extensively applied to analysis of contests over web sites in the desert funnel-weaving spider *Agelenopsis aperta* (Gertsch) (Riechert 1978, 1979, 1984; Maynard Smith and Riechert 1984).

In this study, field experiments were conducted to determine: (1) whether individual *Frontinella pyramitela* (Walckenaer) use assessment strategies with regard to their RHP, i.e., relative size (correlated with fighting ability) and resident status, and (2) whether web size contributes to web site value and is thus related to owner defensive behavior.

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METHODS

Bowl-and-doily spiders, *Frontinella pyramitela*, are often present in large numbers on bushes and low vegetation. The web consists of a non-sticky, bowl-shaped sheet of silk (the bowl) with a flat sheet below (the doily) and an irregular meshwork above (the knockdown structure) which deflects prey into the bowl. The spider rests, venter-up, at the center of the underside of the bowl and waits for prey to fall onto the sheet.

This study was conducted from late April through mid May of 1983 and 1984. Penultimate and adult female *F. pyramitela* were collected from low shrubbery and expanses of ivy planted as ground cover on the University of Georgia campus, Clarke Co., Georgia, then taken to the laboratory for marking and weighing. In the laboratory spiders were placed in a holding device and marked on the ventral side of the abdomen with a small dot of enamel paint. Care was taken not to cover the book lungs or the spinnerets. The mark was visible when the spider assumed its characteristic upside-down position on the web. Spiders were than transferred to gelatin capsules and weighed on a Mettler H10/H20® analytical balance to the nearest hundredth of a mg. Spider mass was recorded and each spider was assigned a number (which was marked on the lid of their vial). Spiders were then refrigerated (7°C) to retard water loss and metabolism, thereby minimizing weight loss and possible hunger-drive states that could influence the results of induced encounters (Ross 1977) (however, nothing was known of the hunger state of spiders prior to capture). An experimental group of five spiders was refrigerated for two days and re-weighed. No change in mass occurred.

Spiders were allowed at least 15 min to warm-up before being taken to the site of an undisturbed population of unmarked individuals. Web dimensions (the longest distance across the bowl and a line perpendicular to it) were measured prior to each interaction. The area of the sheet was later calculated by applying these measurements to the formula for the area of an ellipse (sensu Rypstra 1982). Marked spiders (intruders) were transferred from their vial to a syringe with the end snipped off. The plunger of the syringe was slowly depressed and the spider moved toward the open end, which was held above the knockdown structure of the web. The spider was allowed to crawl down into the webbing. During 1983, behavior was recorded *ad libitum* (Altmann 1974) until one spider left the web or until both spiders ceased movement for five minutes. If spiders had thus become inactive, the web site was marked with flagging tape bearing the intruder's number in waterproof ink. The web site was revisited from three to 24 h later to record the outcome of the encounter and to collect the original owner, if possible. I re-checked web sites until the interaction seemed to be over. The spider that occupied the preferred position at the center of the bowl was considered to be the winner. The loser was most often found high in the knockdown structure or clinging to adjacent vegetation. In 1984, *ad libitum* observations were not made, but additional encounters were initiated and sites were revisited to determine the outcome. The size relationship of the interacting spiders was determined when the original owner was collected and weighed.

In order to estimate if differences in prey availability existed at different web sites, 25 sticky traps were placed beside randomly chosen webs in the area where interactions were performed. These traps consisted of the bottom 6 cm of a

styrofoam cup coated on the outside with Stickem Special® (Seabright Enterprises, Emeryville, California). Traps were fastened (with a clothes-pin), upside-down, to the vegetation near a web. They were set out at 1630 hrs on 17 May 1984 and collected 24 h later. Insects were removed with forceps, identified to order or family, and measured (length in mm). Insects from each trap were wrapped in a piece of filter paper and dried in a drying oven for three days. The dried insects were weighed to the nearest thousandth of a mg on a Mettler H10/H20® analytical balance.

RESULTS

Twelve recognizable behaviors were obvious from *ad libitum* observations of 35 interactions. These were: taste tarsi, groom, search web, pull web, shake web, retreat, advance, lunge, raise legs/wave legs/touch legs, contact, chase, explore web. Most are self explanatory, and are similar to behaviors previously described from bowl-and-doily spiders (Suter and Renkes 1984; Suter and Keiley 1984). "Taste tarsi" was observed in every interaction. Upon introduction into the web, the intruder brought the tarsus of a leg to its mouthparts, and repeated this action with several legs. This was often directly followed by or combined with various grooming behaviors.

The average mass of owner spiders was 6.49 mg (SD = 2.15 mg; $N = 54$), and that of intruders was 6.39 mg (SD = 2.28 mg; $N = 54$). Where size asymmetries existed between opponents, the larger spider was on the average 35% heavier (SD = 15%). In 17 interactions performed, the owner was heavier. In 20, the spiders were of approximately equal size (less than 10% difference in weight). In 17 others, the intruder was heavier. A Chi-square test for independence supports the conclusion that winning was independent of size ($p > 0.50$) (Table 1). Although size does not significantly affect the interaction outcome, resident status does (Table 2). Regardless of what sort of size asymmetry existed, owners won significantly more disputes than did intruders ($\chi^2 = 6.231$; $p < 0.02$) (Table 2). However, closer examination of the data suggests that some size effect may have existed, but because of small sample sizes was not significant. For example, when owners and intruders were of equal size, intruders only won 25% of the interactons, whereas when intruders were heavier than owners they won 41% of the interactions (Table 1).

The average area of a sheet-web used in encounters was 557.43 cm^2 (SD = 288.08 cm^2). There was no significant correlation between the area of the sheet-web and the mass of the owner ($r = 0.078$). No significant difference is apparent in web area between owners which won ($\bar{x} = 547.54$ cm^2, SD = 272.89 cm^2) and owners which lost ($\bar{x} = 577.78$ cm^2, SD = 308.27 cm^2) (Mann-Whitney U test, $p > 0.05$). This suggests that the area of the web had no correlation with the RHP assessment of owners. Though only a short-term estimate, there was some variability in the biomass of prey captured at different web sites (mean dry weight/trap = 0.284 mg, SD = 0.317 mg). The various types of insects captured were: homopterans and hemipterans (1 mm-4 mm), midges (1 mm-2 mm), flies (1 mm-4 mm), wasps (1 mm-3 mm), staphylinid beetles (1 mm), various other beetles (2 mm-6 mm), and thrips (1 mm).

Table 1.—Relationship between size asymmetry and interaction outcome.

Size Relationship	Number of Wins		Conclusion
	Owner	Intruder	
Owner heavier	12 (71%)	5 (29%)	$\chi^2 = 1.164$
Equal weights (within 10% of each other)	15 (75%)	5 (25%)	df = 2, $p > 0.50$
Intruder heavier	10 (59%)	7 (41%)	Accept null hypothesis: winning is independent of spider size.

DISCUSSION

Austad (1983) demonstrated game-playing strategies in male *F. pyramitela*, but female behavior was not examined intensively. However, Suter and Keiley (1984) noted that all agonistic behaviors recorded for males have also been recorded from agonistic interactions between females. Observations of intruder grooming behaviors upon release into a conspecific web suggests that some chemical cue may exist. Since only two interactons were observed outside of contrived situations, perhaps such interactions are actually rare due to some chemical mechanism for detection and avoidance of conspecific webs. Suter and Hirscheimer (in press) have found multiple web-borne pheromones on the webs of *F. pyramitela* females which elicit both courtship and positive geotaxis from males. It may be possible that these chemicals are also detected by conspecific females.

The evidence presented here suggests that web ownership figures significantly in the determination of outcomes of agonistic encounters in female bowl-and-doily spiders. This is contrary to what is known of combat in other spider species. Other studies have found that relative weight, not resident status significantly influences the probability of winning in interactions between females over webs (Buskirk 1975; Ross 1977; Riechert 1978; Wise 1983). However, significant resident advantage was found in combats between male *F. pyramitela* which were closely matched in size (Suter and Keiley 1984). Two factors may explain the owner-biased outcomes observed in the present study. Sheet-webs of the type which *F. pyramitela* builds contain more silk than other types of spider webs (Rypstra 1982). These elaborate webs also have specific substrate requirements for their construction. Rypstra (1983) suggests that such specific substrate requirements may make web sites a limiting resource. In this study, the actual size of the

Table 2.—Effect of weight and resident status on interaction outcome.

	Relative frequency			
	Winner is:			
	Larger	Smaller	Test used	Conclusion
Weight (mg)	19 (56%) ($N = 34$)	15 (44%)	$\chi^2 = 0.4076$ df = 1, $p > 0.50$	Accept null hypothesis: weight bears no significance on outcome.
	Winner is:			
	Owner	Intruder		
Resident status	37 (68%) ($N = 54$)	17 (31%)	$\chi^2 = 6.231$ df = 2, $p < 0.02$	Reject null hypothesis: owner wins more often.

web had no effect on the interaction outcome; owners were more likely to win regardless of the size of their web. I propose that the apparent high value of webs in terms of energy investment and the possibility that web sites are a limiting resource may have selected for generally tenacious defense behavior by web owners in bowl-and-doily spiders. The web is also very important because it is the site of courtship and mating activity.

This study indicates that female bowl-and-doily spiders have little tolerance for conspecific females which invade their webs. However, the degree of tolerance may change under different environmental conditions. For example, observations of possible cohabitation of females in one web (Weger and Tietjen 1984) may have occurred under higher prey density conditions than existed in the present study. It is not yet clear, however, whether these were examples of tolerance of conspecifics or were agonistic interactions in progress. In contrast to these results, a study by Suter (1985) found that males often cohabit with females for long periods of time, but does not report any observations of females cohabiting. Male linyphiids are unusual among male spiders in that they feed frequently, and temporarily use female's webs for this purpose. A difference in the context of communication signals (reproductive rather than aggressive by the male) as well as potential benefits to the female by a reduced probability of death through predation by theridiid or mimetid spider predators (Suter 1985) accounts for this special case of temporary tolerance.

Though some variability in prey abundance existed between web sites in the present study, the significance of this variability is difficult to assess. It would seem that most of the owners were at sites that at least met their requirements, otherwise it would be predicted that they would abandon rather than defend the web. Linyphiids are known to abandon web sites in response to low prey levels, even without the added factor of web intrusion (Martyniuk 1983). It is also possible that the availability of web sites with respect to population density may affect spacing patterns and tolerance of conspecifics. Janetos (1984) found that an abundance of web sites at his study area made competitive interactions unprofitable. As in this study, he never observed female bowl-and-doily spiders cohabiting in webs.

Within-species variation in aggressive behaviors has also been seen in other spiders (Riechert, in press). Two populations of the spider *Agelenopsis aperta* have been shown to have differences in behavior with a genetic basis. These differences are associated with differences in microclimate and prey density between the different habitats occupied (Riechert 1978, 1979). Rypstra (1983) has shown that spider species which are normally solitary will increase tolerance of conspecifics when provided with high food levels and numerous web sites. Evidence provided by several different studies on bowl-and-doily spiders indicates that some variation exists in levels of tolerance for conspecifics and the occurrence of intraspecific interactions (Janetos 1984; Weger and Tiejen 1984; Suter 1985; present study). Additional studies of this variation under differing conditions of web site and prey availability may provide further evidence that some spiders are able to alter their defensive strategies as changes occur in the costs and benefits associated with engaging in an agonistic encounter.

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